CHAPTER 1

Plant–Animal Coevolution: A Synoptic View of the Paleozoic and Mesozoic

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I. Introduction

Evolution is a continuing, though erratic process. Aeons of gradual change in the morphology, anatomy and chemistry of any given class of organisms are suddenly interposed by catastrophic extinctions and equally dramatic radiations. In many cases such changes, either gradual or sudden, have been ascribed to variations in physical factors, such as temperature, UV light intensity, atmospheric oxygen concentration and so on. There appears to be a tendency to forget, however, that a major lasting change in the distribution, diversity or numbers of any given taxa of animals or plants will usually have

profound effects on all other organisms in the surrounding ecosystem. Such interlocking chains of events can be seen readily today in the man-made eutrophification and pollution of lakes and rivers. We may conclude, therefore, that evolutionary changes in any given phylum of animals and plants should not be discussed as though each one existed in isolation or, at best, in association with a few like groups with which it competed for lebensraum. Instead, we must firmly think of evolution as indicative of a concerted change in many kinds of organisms. By this I do not wish to imply that there is necessarily always a definable sequence of events occurring over a limited time span, nor that a given cause of change exerts exactly the same effect in widely different geographical areas, but we should always be aware and account for events where possible in coevolutionary terms.

It is true that, recently, following the splendid example of Ehrlich and Raven (1965) on the coevolution of butterflies and flowering plants, many articles have been published purporting to draw attention to similar coevolutionary phenomena (see Gilbert and Raven, 1975; Wallace and Mansell, 1976). In truth, however, with few exceptions (e.g. Smart and Hughes, 1973; Kevan *et al.*, 1975), most authors have missed the message put out by these two pioneers and have mistakenly assumed that a description of the biochemical or other aspects of present-day ecological interactions can explain the changes which have taken place in the remote past. This is not to say that a closer study of existing ecological situations is not extremely important in our attempts to understand the course of evolution. Nevertheless, it is shortsighted, to say the least, to suggest that the biochemical or other constraints which are placed on plant–animal interactions today have existed for all time. Nor, in my opinion, is it sensible to concentrate, as most authors have done (cf. contributors to Gilbert and Raven, 1975), only on angiosperms and modern insects for they are much too closely interlinked to explain all evolutionary processes.

What is really required is an overall synoptic view of plant–animal coevolution and this I have attempted to provide in this chapter. Obviously, there are many imperfections and omissions in this approach, most of which arise from my own ignorance. To me, this is of little consequence if I manage to stimulate some to think more deeply about the overall problems involved.

I have concentrated solely on the biochemical aspects of coevolution since the Silurian. To go back further, one would need to consider ecological changes in ancient aquatic ecosystems whose modern counterparts are still poorly known. Nevertheless, we do eventually need to consider the importance of such events in determining how and for what reasons colonization of the land occurred. One essential problem is the role of early soil-forming organisms, perhaps algae, fungi and a range of protozoans and simple metazoans. Another, is the variation in cell wall biochemistry which led to the development of cuticle in non-vascular plants early in the Silurian. Both were

essential elements in the sea–land transformation which presumably took placé via amphibious forms.

II. The Early Paleozoic

A. PLANT EVOLUTION

The events leading to the colonization of land by plants are now fairly well established (Banks, 1970; Chaloner, 1970). Transit onto land must have been preceded by colonization of many terrestrial sites with impeded drainage or by the sides of streams or in the intertidal zones with a significant microflora and fauna consisting of algae, fungi and protozoa. Many paleobotanists subscribe to the view that certain heterotrichous members of the Chlorophyta, for example the Chaetophorales, were actually ancestral to the true land forms (Banks, 1970). Kevan *et al.* (1975) suggest that many non-vascular plants with a cuticle-like covering and resistant spores may have preceded the earliest vascular plants or at least accompanied them onto land in the early Devonian period.

With revised dating of some early fossil plant records, the evolutionary development of the first vascular plants is much clearer than it was a few years ago. The earliest land plants lacked differentiation into leaves, stems and roots and had sporangia at first terminally and later laterally on the axes. The earliest tracheophyte flora of which we have detailed anatomical data is that of the Rhynie Chert of the late lower Devonian. This contains fossils of two lines of vascular plants (*Rhynia*, a psilopsid and a lycopod-like forerunner). In general other fossil evidence, including chemical (Niklas and Gensel, 1977), points to the fact that the Psilopsida and Lycopsida both appeared and were diversifying during the early Devonian.

The evolution of green plants was paralleled in the Devonian by equivalent changes in the fungi (Kevan *et al.*, 1975). Here there is a strong association with plant hosts. Many remains of Devonian land plants contain abundant evidence of fungal mycelia and hyphae. Most of these early fungal land plant colonizers seem to be Phycomycetes. It has been suggested that it was only by growth as internal parasites that fungi could leave their original wholly aquatic habitats and start a subaerial existence (Kevan *et al.*, 1975). The fossil records of the semi-independent Ascomycetes and Basidiomyetes do not appear until the upper Carboniferous.

B. ANIMAL EVOLUTION

Kevan *et al.* (1975) have comprehensively reviewed the origins of the terres-

(arachnids) in the early Devonian. The earliest true fossil insects are the primitive collembolans (springtails), again in the Rhynie Chert. Fossils of winged insects are not found until the late Devonian, concomitant with the development of arborescent plants (Smart and Hughes, 1973). Other terrestrial animals which may be of importance to our thesis did not develop until later. The gastropods (snails), which are important plant grazers today, did not evolve onto land until the Upper Carboniferous but marine forms and other aquatic molluscs undoubtedly were important earlier in intertidal zones (Schrock and Twenhofel, 1953). The first land vertebrates, the amphibia, did not arise until the close of the Devonian (Young 1962).

C. PLANT, ANIMAL AND FUNGAL COEVOLUTION

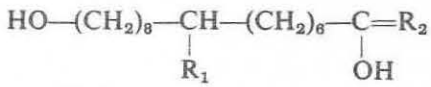
We now have convincing evidence for the coevolutionary development of the early terrestrial vascular plants, arthropods and the fungi (Kevan *et al.*, 1975). It has been postulated that while most myriapods fed only on plant detritus, many of the Devonian Chelicerates, although mainly carnivorous, were perhaps also facultative herbivores. The fossil remains of these animals indicates they had mouth parts which could pierce plant stems and spores. Kevan *et al.* (1975) pointed out that the fossils of *Rhynia* show several empty sporangia containing fragments of arachnids. The Rhynie plants also show a number of stem lesions evidently inflicted while they were still alive, many of which appear to be associated with fungal activity. On the basis of this evidence, Kevan and his co-workers concluded that, in the Devonian, many insects fed on spores, spore protoplasts and plant sap and that the large changes which took place in spore size and spore-wall structure during this period originated as defences against these herbivores. The characteristic spiny stems (which are found in a number of otherwise distinct Devonian plants) and of arborescence (which preceded the arrival of alate arthropods) was likewise ascribed as a defence against insect attack. The importance of insects as spore dispersers was also stressed and it was suggested that the origin of heterospory may have been connected with this arthropod mediated fertilization (Kevan *et al.*, 1975). Fungi of this period were postulated as phytopathogens, presumably carried by arthropod vectors. So the whole system of plants, insects and fungi, is believed to have coevolved together.

Of course, it is possible that heterospory may have evolved independently of arthropod mediated fertilization and that changes in spore ornamentation equally might have arisen originally as an anti-fungal mechanism. Either way, the fact remains that the changes in plant architecture were called into play as defences against other organisms in the ecosystem.

D. BIOCHEMICAL EVOLUTION

1. Lipid and Terpenoid Compounds

Changes in the biochemical constituents of plants in the early Paleozoic were as dramatic as the changes in spore size or stem morphology. I have already mentioned the development of the cutin. It is noteworthy that psilophyte cutin has a different structural composition than that of other land plants (Caldicott *et al.*, 1975) in that it contains hexadecane triols (1). Other



(1) $R_1 = OH$; $R_2 = H_2$; 1,8,16-Hexadecane triol
(2) $R_1 = H$; $R_2 = O$; 16-Hydroxyhexadecanoic acid

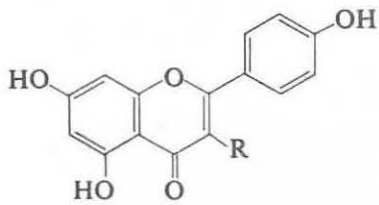
primitive plants which have been examined, mosses, lycopods and ferns, have cutins containing only traces of mono- or dihydric alcohols, the usual constructents being hydroxyhexadecanoic (2) or octadecanoic acids (Holloway, 1973; Hunneman and Eglinton, 1972). The significance of this change in coevolutionary terms, however, cannot be deduced on present knowledge.

Undoubtedly, changes in the complement and diversity of sesqui-, di- and triterpene components of the early land plants (Porter and Markham, 1978) were also important in determining their evolutionary success, but again we have too little evidence as to the ecological importance of these observations.

Let me turn, therefore, to biochemical changes which appear to be of greater consequence in the coevolution of early land plants and their competitors. One of these is the observed large increase in the amount of sporopollenin in the spore walls (Swain, 1974). For example, the spore walls of Chlorophyta and of fungi contain either no sporopollenin (*Prasinocladus*) or less than 50% of this resistant component, whereas the lycopods (no psilophyte spore data are available) have over 90%. This change must have had profound effects on spore longevity, resistance to desiccation and fungi and to arthropod feeding.

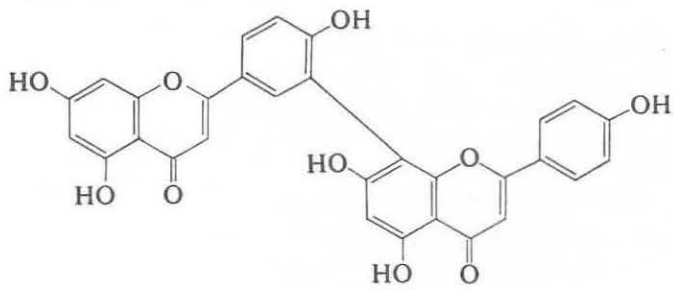
2. Phenolic Compounds

Perhaps the most important biochemical changes which occurred in plants, as they evolved on land, were those which occurred in their complement of phenolic compounds. For example, most Chlorophyta and all fungi lack flavonoids. Yet these compounds and the related cinnamic acids, are present in all present-day land plants (Swain, 1974). It has been suggested that these compounds (e.g. 3, 4) first evolved as UV light screens (Swain, 1971) but it



(3) R = H; Apigenin
(4) R = OH; Kaempferol

seems probable that rather rapidly (by evolutionary time) their potential use as anti-fungal (Friend and Threlfall, 1976) and anti-insect agents (Swain, 1977) came to be fixed in plants by selection. Thus it is of interest that the biflavones (e.g. 5), the only flavonoid components present in *Psilotum* (pre-



(5) Amentoflavone

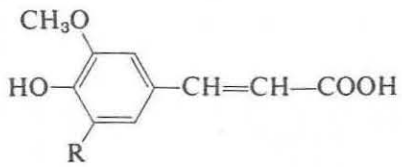
sumably related to *Rhynia* and *Sawdonia*) occur in the cell walls of the tracheids of this plant suggesting that the compounds are present to protect the inner cell walls from hydrolytic attack by fungal enzymes (Cooper-Driver and Swain, unpublished results).

Similarly, the other present-day existing psilophyte, *Tmesipteris*, is reported to contain copious amounts of phenolic pigments in the cutin (Caldicott *et al.*, 1975) again suggesting an anti-fungal (or an anti-insect) function.

Perhaps even more important for determining the success of early land plants was the evolution of the aromatic acid acylation of the polysaccharide components of the cell wall. This appears to be an ancient land-plant feature (Friend, 1976). In many marine algae, polysaccharide components of the cell wall are acylated by sulphate. As with the acetylation of the amino polysaccharides of bacteria and fungi, this presumably slows down the rapidity of cell-wall hydrolysis and hence attack by invading pathogens or herbivores. However, it is likely that coevolution of acyl hydrolysases, sulphatases and acetylases in potential pathogens had already occurred prior to the Silurian and that the land plants needed to evolve a new defensive strategy. The utilization of hydroxy/methoxy benzoic and cinnamic acids (e.g. 6) as acylat-

ing agents of the cell wall polysaccharides presumably supplied this need. Certainly cellulose and hemicelluloses are protected from rapid breakdown by fungal hydrolases by such substitution (Hartley, 1973). While this protection is not absolute – fungal hyphae eventually can penetrate cell walls – it has apparently been of sufficient importance to be maintained in flowering plants.

The phenolic acid acylation of cell wall polysaccharides is of perhaps even greater importance in evolutionary terms than mere protection against pathogens. The initial substitution on the cell wall, which we can think of as a "barbed wire" defence of the cell wall carbohydrates, may well have led to the origin of lignification and its important consequences in the development of arborescent forms. It is generally believed that lignin is formed by the random peroxidase-polymerization of suitably substituted cinnamyl alcohols such as coniferyl alcohol (Swain, 1974). While it is probably true that such compounds play an important part in the elaboration of the final structure of lignins, it appears possible that they do not, in fact, act as the initial building stones. There seems reason to believe that these may have originally arisen by cross-linking of adjacent ferulyl (or other substituted cinnamyl) groups attached to the cell wall polysaccharide matrix. The rest of the polymer would then be attached to these "starter" molecules by the reactions outlined above. This fact would account for the occurrence of lignin–polysaccharide complexes which are usually obtained when no strong acids or bases are used in the isolation of the phenolic polymer. These ideas have been substantiated recently by the isolation of ferulyl dimers from cell wall polysaccharide preparations (Hartley *et al.*, 1976). It is also of interest that the Psilopsida has lignin based on the simpler *p*-coumaryl pattern, while the lycopods have either ferulyl or sinapyl-type lignins (Swain, 1974), the latter being generally regarded as indicative of flowering plants! This undoubtedly indicates that evolutionary pressures have been at play, since the methoxycinnamic acids (ferulic (6) and sinapic (7)) are probably less easily degraded by micro-



(6) R = H; Ferulic acid
(7) R = OCH_3; Sinapic acid

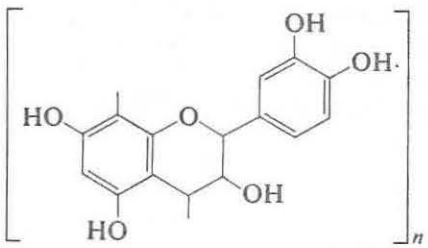
organisms than is *p*-coumaric acid and can themselves inhibit growth of both plants and fungi (Swain, 1977).

All these changes in phenolic biochemistry which most probably occurred in primitive land plants during the Devonian demonstrate the prime

importance of the biosynthetic pathway leading to substituted cinnamic acids via phenylalanine. On the one hand, this would give rise directly to anti-fungal protection of cell walls and thence to lignin while, on the other, it would lead to the more useful flavonoid UV light screens and antibiotics. Such features could explain much about the obvious success of Devonian plants.

Let us return to the flavonoids. The modern lycopods probably represent three separate offshoots of the line of plants bearing lateral sporongia and this is borne out by their flavonoid (and lignin) chemistry. The Selaginellales, like *Psilotum*, produce only biflavonoids whereas the other two groups (Lycopodiales and Isoetales) have simple flavones (Voirin and Jay, 1978). The latter, assuming they were present as glycosides, might have evolved originally as insect feeding deterrents or attractants (cf. Schoonhoven, 1972), either by their "taste" or by their being laid down in sporangial guides visible to insects in the UV.

The most important change in flavonoid chemistry during the late Devonian was the ability of the Sphenopsida to synthesize 3-hydroxy derivatives. The fact that this feature is also found in mosses and liverworts (Porter and Markham, 1978) indicates, to me, that the bryophytes can definitely be ruled out as ancestral to the primitive tracheophytes and, indeed, may have arisen as a reduction from some more advanced, extinct sporophyte line. The ability to introduce the 3-hydroxyl group into the flavonoid molecule leads to the possibility of producing flavonols (e.g. kaempferol, 4) which give a wider array of visible and UV signals for the guidance of arthropod spore dispersers. More importantly, however, this biosynthetic step can also lead to the production of the proanthocyanidin or condensed tannins (8). These



(8) Procyanidin (Condensed tannin)
$n = 2$–6

latter compounds are undoubtedly the most useful of all plant chemical defences. Not only are they potent anti-fungal, anti-bacterial and even anti-viral agents (Swain, 1977) but they bestow on plants which have the ability to synthesize them a powerful feeding deterrent to all herbivores (Swain, 1976, 1977; Oates *et al.*, 1977; Cooper-Driver *et al.*, 1977; Feeny, 1976; Rhoades and Cates, 1976).

These phenolic polymers, of MW 1000–2500 daltons or larger, act through

their ability to combine with protein (and other hydrogen-bonding polymers) and thus inhibit enzymes and reduce the nutritionally available protein in foods. The compounds are very difficult to degrade and their molecular size renders them almost impossible to sequester into vesicles so that their activity may be aborted. Because of these facts, it is not surprising to find that they are still of considerable importance in today's ecosystems (Swain, 1977).

E. CONCLUSIONS

We may conclude, therefore, that the increase in the complexity of biochemical pathways during the Devonian well supports the fifty-year-old suggestions made by Tillyard (1928) that "the evolution of true insects (*to which we may add fungi and perhaps molluscs*) . . . was taken through an ecological association with the special group of plants which made their footing on the dry earth". We can add more. The ability to produce, chemically, more resistant spores and cell walls, to synthesize lignin and general purpose antibiotics and feeding deterrents was as important in the evolution of early plants as advances in their anatomy or morphology (Table I). Without such chemical changes the arborescent forms of the coal-swamp flora could not have evolved at all.

III. The Carboniferous Period

A. PLANT AND ANIMAL EVOLUTION

The Carboniferous saw the rise of all modern plant Divisions except the angiosperms and was dominated by the giant arborescent forms which developed in the late Devonian (Chaloner and Lacey, 1973). By the end of the Paleozoic era ferns, seed ferns, conifers, Cordaitales, ginkgos and cycads were all important features of the landscape having displaced the giant lycopods and sphenopsids of the Carboniferous. Animal evolution was equally extensive. The amphibia reached their zenith as the dominant class of land vertebrates in the Lower Carboniferous and were gradually displaced by the reptiles (Labyrinthodonts and stem reptiles) by the end of the upper Carboniferous. The available evidence suggests that the dominant amphibia were all carnivores and even if this were not so their necessary riparian existence meant that late Paleozoic plants could evolve away from such aquatic habitats, without predation from this group of vertebrates.

The main herbivores of the Carboniferous were likely to have been the insects which, by then, had acquired flight and all the modern groups, except the paraneopterus and mecopteroid stocks (Smart and Hughes, 1973), were in existence. In spite of this evolutionary success, it is obvious from the extensive coal-swamp remains of the Carboniferous that plants were not totally

TABLE I

Changes in defence and predators of Devonian plants

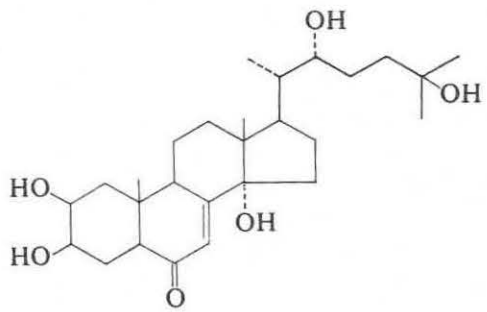
M.y.a.[a]	Plant group	Chemical defence		Potential predators		
		Tannins	Diterpenes	Fungi	Insect	Other
400	Psilopsida	–	–	Phycomycetes	Centipedes	Molluscs Worms
380	Lycopods	–	–		Mites	
	Horsetails	+	–		Springtails	
375	Ferns	+ + + +	+ +			
370	Gymnosperms	+ + +	+ + + +	Rusts		
360	(Arborescent forms; lycopods and ferns)				Winged insects	Amphibia
345 (300 Carboniferous)	(Many arborescent forms)			Basidiomycetes		

[a] First known fossils.

consumed. There appears to be no morphological or anatomical justification for this. The Carboniferous flora should have been as edible as its Devonian antecedent. The advantage given to plants to escape spore predation by their ability to develop arborescent forms, in which the spores were borne 30 m or more from the ground, should have been rapidly diminished by the evolution of the giant winged insects of the Carboniferous.

B. BIOCHEMICAL EVOLUTION

If the outline of plant and animal evolution given above is true, what was the cause of this worldwide 60 million year period of apparent plant supremacy? There are probably at least three reasons. The first is the ability of the coal-swamp flora not only to grow out of reach of most of its potential spore eaters but for many to protect themselves against fungal attack by the production of tannins, especially in the lignified dead cells of the stele (heartwood); the second is the increasing protection of the haploid thallus against attack by fungi, perhaps because of increased production of cinnamic acid derivatives (cf. Cooper-Driver, 1977); the third is the production of ecdysone analogues (e.g. 9) and, perhaps, other hormone mimics which would greatly interfere with insect metamorphosis (Williams, 1970; Cooper-Driver, 1976; Swain and Cooper-Driver, 1974).



(9) α-Ecdysone

The main arguments relating to the first of the proposals outlined above have been presented earlier. It only suffices to say that the Sphenopsida and all families of ferns, with the exception of the Ophioglossales, contain copious amounts of procyanidins (8) and are extensively lignified. The second proposal rests on the observed ability of fern thalli to grow readily in the presence of many different kinds of fungi (Hutchinson, 1976) and the unexpected finding that they contain no tannins (Cooper-Driver, 1977). We can presume, therefore, that the large amounts of cinnamic acids may account for their immunity, although other classes of compound should also be examined.

The third relates to the fact that ecdysone analogues (9) are not only widespread in ferns but occur in concentrations often over a million times higher than that in the insects themselves (Williams, 1970). While the role of ecdysones as feeding deterrents is not by any means proven, it seems highly likely that the development of many herbivorous insects would be directly affected if they ingested sufficient amounts of these, unless the insects had evolved a clearly discriminatory barrier to the uptake of these compounds in contrast to other needed sterols.

It may be postulated that late Carboniferous insects never successfully overcame all these chemical defences and, hence, the world had to wait until more versatile herbivores arose, before the plants succumbed.

IV. The Permian Period

The important event which probably brought about the changes in the land flora in the Permian was the evolution of large herbivorous reptiles. These animals, with their independence of riparian environments, could range widely. It is unlikely that they would have been affected by the main hormonal (ecdysone) defences of the remaining mature plants which had evolved in the Carboniferous and since young sporophytes of the existing flora were probably devoid of lignins or tannins, these animals could have had a devastating effect on plant survival.

These facts alone might account for the demise of the lycopods and sphenopsids. The early gymnosperms and their allies might have survived, however, not only because of the evolution of the seed habit, but by their possession of more potent mono-, sesqui- or diterpenoid feeding deterrents. These classes of compounds could have been important in keeping late Paleozoic insects at bay in the same way, as happens today (Swain, 1977). Certainly, the diversity of structures found in modern day gymnosperms is in marked contrast to the ferns, many of which contain few, if any, of such compounds.

V. The Mesozoic

A. PLANT AND ANIMAL EVOLUTION

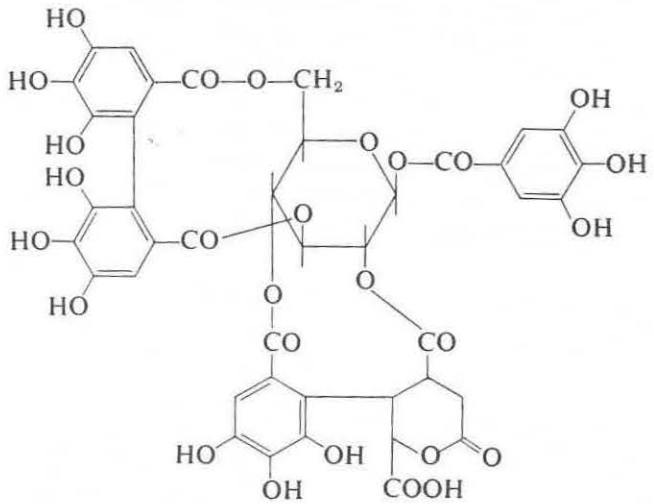
The extinctions at the end of the paleozoic era were profound and cannot be explained satisfactorily on either morphological or chemical grounds. Many of the predominant plants and animals of the Permian were superseded (Kummel, 1970). All one can assume is that some profound climatic change

was the cause. However, there appears to have been few gross differences in the chemical palatability of the plants which took over from the extinct forms or in their acceptibility to the new orders of reptiles.

The Mesozoic is, of course, the age of reptiles. In spite of further extinctions at the end of the Triassic, one major group of this class, the ruling reptiles or dinosaurs, became the faunal dominants of the land for over 160 million years. What then caused their demise at the end of the Mesozoic Era? Again one might point to the various climatic changes which took place, but one fact stands out. The extinction of the dinosaurs (but not other mainly carnivorous small reptiles; crocodiles and snakes) is inversely related to the rise of the flowering plants (Swain, 1976). It is apparent that the latter arose about 120 million years ago and their evolution has been recently well reviewed (Barnard, 1973; Hughes, 1973; Penney, 1969).

B. BIOCHEMICAL EVOLUTION

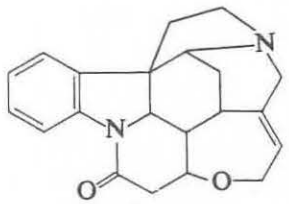
From the point of view of the deterrent chemicals they produce, angiosperms can be divided into two diverse lines. The first, exemplified by the Hamamelidae, Rosidae and Dillenidae produce hydrolysable tannins (e.g. 10) which are more efficient than the earlier compounds of this class, the



(10) Chebulagic acid (Hydrolysable tannin)

condensed tannins, as anti-fungal agents or feeding deterrents since they are effective at only about one-tenth of the concentration of the latter. Furthermore, the hydrolysable tannins are biodegradable and thus can be rapidly recycled by the plant if necessary (Swain, 1976). The second line, represented by the Magnoliidae and related angiosperm subclasses, concentrated on

alkaloids (e.g. strychnine, 11) as feeding deterrents. This group of compounds is almost entirely absent from all lower plants except the lycopods. It may be



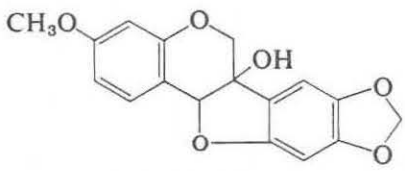
(11) Strychnine

presumed, from the evidence of reptile feeding habits, that these two chemical strategies were deleterious to the survival of these animals in the late Cretaceous when the flowering plants became the dominant part of the flora (Swain, 1976).

The reasons are quite plain. Herbivorous reptiles are more readily deterred by plants containing equal amounts of hydrolysable tannins than those containing the corresponding flavonoid-based condensed tannins which are symptomatic of the earlier Mesozoic floras. However, these animals appear to be unable to detect, by taste, alkaloids at concentrations which might be physiologically deleterious to them (Swain, 1976).

It must be concluded, therefore, that the changes in chemical defences which the flowering plants possess did have a profound effect on the survival of the ruling reptiles in the late Cretaceous. Other factors may have been of equal importance but these chemical changes should not be ignored.

The same is true for the development of angiosperm anti-fungal defences. The changeover from proanthocyanidin tannins to hydrolysable tannins was obviously of importance. However the evolution of "on-demand" antibiotics, the phytoalexins (e.g. pisatin, 12) were equally important (Friend



(12) Pisatin

and Threlfall, 1976). These compounds, so far consisting of only three types (flavonoid, terpenoid, acetylenes), are produced only when the pathogen actually penetrates into the plant (see chapter 14). They thus confer a great advantage by sparing the plant's energy budget.

Besides the classes of compounds mentioned above, the angiosperms have developed many, apparently unique, chemical defence mechanisms: glucosinolates, novel terpenoids including iridoids, many new non-protein

TABLE II

Evolution of defensive chemicals in plants

Class of compound	Defence against[a]				Plant class[b]				
	Pl	Ph	Ins	Vert	Psilotum (400)	Horsetails (370)	Ferns (320)	Gym (200)	Ang (70)
Phenolics									
Simple	+	+	−	(+)	+	+	+	+	+
Tannins	+	+	+	+	−	(+)	++	++	++
Isoflavonoids	−	+	−	−	−	−	−	−	+
Terpenoids									
Mono-	+	−	+	+	−	−	−	++	++
Sesqui- and Di-	(+)	+	+	+	−	−	+	++	++
Tri-	?	−	+	+	−	−	+	++	++
N-Containing									
Non-protein Amino acids	+	+	+	+	−	−	+	(+)	+
Alkaloids	−	(+)	+	+	−	−	−	(+)	++
Cyanogenic glycosides	−	−	+	+	−	−	(+)	(+)	+
Glucosinolates	−	−	+	+	−	−	−	−	+

[a] Pl = plants (allelopathy); Ph = phytopathogens (fungi, bacteria, viruses); Ins = insects; Vert = vertebrates; Gym = gymnosperms; Ang = angiosperms.

[b] Number in brackets = million years ago age of dominance.

amino acids (see chapter 6), lectins, and others. Most of these have been discussed in earlier reviews (Swain, 1977; Gilbert and Raven, 1975; Wallace and Mansell, 1976) and need not be covered here. Nevertheless they all need to be considered in order to understand the restless tide of evolutionary change (Table II).

VI. Conclusions

In this short chapter, I have ignored or only cursorily discussed many aspects of plant chemistry which must have had profound effects on the coevolution of plants and animals. For example, the alkaloidal compounds of the lycopods and sphenopsids: did these evolve as feeding deterrents in the Devonian or later? The same type of question can be asked of cyanogenesis in the few ferns which contain this feature (Harper *et al.*, 1976) and the bitter sesquiterpenoid lactones of the ferns and gymnosperms. It is equally true to say that I have ignored, often deliberately, many finer points of plant and animal evolution. For example, the many significant changes in the morphology, anatomy and physiology of plant defensive mechanisms and the equivalent changes in animals which have taken place over the past 400 million years. Nevertheless, I believe that the continued thread of diversity in the nature of plant chemical constituents provides the most vital force in plant–animal coevolution.

ACKNOWLEDGEMENTS

I wish to acknowledge my debt to Professor W. G. Chaloner, University of London, who not only presented this paper at the Symposium, but also made many suggestions for its improvement. I am also grateful to Professors Barry Cameron and Arthur Brownlow, both of Boston University, for their help and guidance. Finally I wish to thank Ms. Audrey McNamara for careful preparation of the manuscript.

REFERENCES

Banks, H. P. (1970). "Evolution and plants of the past". Belmont, Calif.

Barnard, P. D. W. (1973). *In* "Organisms and continents through time" (Hughes, N. F., ed.), pp. 175–187. Palaeontological Association, London.

Caldicott, A. B., Simoneit, B. R. T. and Eglinton, G. (1975). *Phytochemistry* **14**, 2223–2228.

Chaloner, W. G. (1970). *Biol. Rev.* **45**, 353.

Chaloner, W. G. and Lacey, D. (1973). *In* "Organisms and continents through time" (Hughes, N. F., ed.), pp. 271–289. Palaeontological Association, London.

Cooper-Driver, G. A. (1976). *Bot. J. Linn. Soc.* **73**, 35.

Cooper-Driver, G. A., Finch, S., Swain, T. and Bernays, E. (1977). *Biochem. Syst. and Ecol.* **5**, 177.
Ehrlich, P. R. and Raven, P. H. (1964). *Evolution* **18**, 586.
Feeny, P. (1976) *Rec. adv. phytochem.* **10**, 1.
Friend, J. (1976). *In* "Biochemical Aspects of Plant–Parasite Relationships" (Friend, J. and Threlfall, D. R., eds), pp. 291–304. Academic Press, London and New York.
Friend, J. and Threlfall, D. R. (eds) (1976). "Biochemical Aspects of Plant–Parasite Relationships". Academic Press, London and New York.
Gilbert, L. E. and Raven, P. H. (eds) (1975). "Co-evolution of animals and plants". Univ. of Texas Press, Austin.
Harper, N. L., Cooper-Driver, G. A. and Swain, T. (1976). *Phytochemistry* **15**, 1764.
Hartley, R. D. (1973). *Phytochemistry* **12**, 661.
Hartley, R. D., Jones, E. C. and Wood, T. M. (1976). *Phytochemistry* **15**, 305.
Holloway, P. J. (1973). *Phytochem.* **12**, 2913.
Hughes, N. A. (1973). *In* "Organisms and continents through time" (Hughes, N. F., ed.), pp. 189–198. Palaeontological Association, London.
Hunneman, D. M. and Eglinton, G. (1972). *Phytochemistry* **11**, 1989.
Hutchinson, S. A. (1976). *Bot. J. Linn. Soc.* **73**, 145.
Kevan, P. G., Chaloner, W. G. and Savile, D. B. O. (1975). *Palaeontology* **18**, 391.
Kummel, B. (1970). "History of the earth", 2nd Edn, Freeman, San Francisco.
Niklas, K. and Gensel, P. G. (1977). *Brittonia* **29**, 100.
Oates, J. F., Zantovska, J. and Swain, T. (1977). *Biochem. Syst. and Ecol.* **5** 317.
Penney, J. S. (1974). *In* "Aspects of Palynology" (Tschudy, R. H. and Scott, R. A., eds), pp. 331–376. Wiley-Interscience, New York.
Porter, R. and Markham, K. (1978). *Prog. in Phytochem.* **5** (in press).
Rhoades, D. F. and Cates, R. G. (1976). *Rec. adv. phytochem.* **10**, 168.
Schoonhoven, L. (1972). *Rec. adv. phytochem.* **4**, 197.
Schrock, R. R. and Twenhofel, W. H. (1953). "Principles of invertebrate evolution", 2nd Edn. McGraw-Hill, New York.
Smart, J. and Hughes, N. F. (1973). *In* "Insect–plant relationships" (van Emden, H. F., ed.), pp. 143–155. Blackwell, Oxford.
Swain, T. (1971). *In* "Molecular evolution" (Schoffeniels, E., ed.), Vol. 2, p. 274. North Holland, Amsterdam.
Swain, T. (1974). *In* "Comprehensive Biochemistry" (Florkin, M. and Stotz, E. H., eds), pp. 125–453. Elsevier, Amsterdam.
Swain, T. (1976). *In* "Morphology and biology of reptiles" (d'A Bellairs, A. and Cox, C. B., eds), *Linn. Soc. Sym. Ser.* No. 3, p. 102.
Swain, T. (1977). *A. Rev. Pl. Physiol.* **28**, 479.
Swain, T. and Cooper-Driver, G. A. (1974). *In* "Phylogeny and classification of ferns" (Jermy, A. C., ed.), pp. 111–134. Linn. Soc., London.
Tillyard, P. (1928). *Trans. ent. Soc. London* **76**, 65.
Voirin, B. and Jay, M. (1978). *Biochem. Syst. and Ecol.* **6** (in press).
Wallace, J. W. and Mansell, R. L. (eds) (1976). *Rec. Adv. Phytochem.* **10**, 1.
Williams, C. H. (1970). *In* "Chemical Ecology" (Sondheimer, E. and Simeone, J. S., eds), pp. 103–132. Academic Press, New York.
Young, J. Z. (1962). "The life of vertebrates", 2nd Edn. Oxford Univ. Press, Oxford.